

Differential infanticide by adult curly-tailed lizards, *Leiocephalus schreibersi*

THOMAS A. JENSSEN*, DALE L. MARCELLINI†, KURT A. BUHLMANN*
& PAUL H. GOFORTH*

* *Biology Department, Virginia Polytechnic Institute and State University, Blacksburg,
VA 24061, U.S.A.*

† *National Zoological Park, Smithsonian Institute, Washington, D.C. 20008, U.S.A.*

Abstract. The curly-tailed lizard is a ground-dwelling, territorial species, whose home range areas were stable and averaged 79 m² (males), 43 m² (females) and 6 m² (juveniles). Every male had one to three females within his home range. The average home range overlap varied within and between age and sex classes, from 8% of male home range areas overlapping with juvenile home ranges to 100% of juvenile home ranges coinciding within male home ranges. Except for three, each of the 24 juveniles on the study area was exclusively associated with an adult male and female whose territorial behaviour prevented access of other adults to the juvenile. This was significant because 36% of the tested resident adults (three males, six females) attacked tethered conspecific juveniles and were considered cannibals. All 24 resident juvenile home ranges were within non-cannibal adult home ranges. Only three juveniles were at risk by having their home ranges also overlapped by a cannibalistic adult. No adult-free refugium existed for juveniles as their separation distances from non-cannibalistic adults averaged 1.0 m (cannibals had no juveniles nearby). Our data indicate that: (1) exploitative infanticide may be a prime source of juvenile mortality; (2) stable, coinciding territories of a non-cannibalistic adult male and female provide associated juveniles with protection against cannibal adult interlopers; and (3) 88% of resident juveniles were being protected from possible cannibalism by only 30% of the adults on the study area.

Infanticide, the elimination of embryonic or immature forms by conspecifics, has long been considered pathological, possibly caused by the stress of overcrowding, or simply by rare instances of accidental or opportunistic feeding. Only in the last decade has intraspecific killing and cannibalism been shown to occur in more than 1300 species of vertebrates and invertebrates (reviews of Fox 1975; Polis 1981; Hausfater & Hrdy 1984; Polis et al. 1984; Cockburn 1988). For some species, infanticide appears to be of ecological and evolutionary significance. Hrdy & Hausfater (1984) and Huntingford & Turner (1987) summarize the adaptive functions of infanticide as being: (1) exploitation of immatures as food; (2) elimination of immatures as potential competitors for limited resources; (3) improved breeding opportunities for killers by removing non-related and dependent immatures of prospective mates; and (4) improved inclusive fitness of parents by their selective killing of offspring.

Even though infanticide has been much studied

in vertebrates, the extent of its occurrence and the consequences of any selected benefits are still unknown in reptiles. In a recent comprehensive symposium on infanticide (Hausfater & Hrdy 1984), no studies dealt with reptiles. Specific literature surveys of reptilian conspecific predation (Polis & Myers 1985; Mitchell 1986) have reported instances in 49 and 191 species, respectively. However, these accounts were primarily anecdotal and offered little or no data to support the frequency or significance of conspecific predation.

Anecdotal and indirect evidence of infanticide continue to be reported for reptiles (e.g. Auffenburg & Auffenburg 1988); however, to our knowledge the present study on *Leiocephalus schreibersi* provides the first field data and experiments that suggest that conspecific predation is a prime cause of juvenile mortality in a reptilian species. Furthermore, our data show that the adult propensity for infanticidal behaviour was very definite, individual-specific, and restricted to a third of the observed population.

MATERIALS AND METHODS

Leiocephalus schreibersi live in the xeric coastal regions of Hispaniola (Schwartz & Thomas 1975). They are sexually dimorphic in size; mean (\pm SE) snout-vent lengths (SVL) for 13 adult males and 14 females were 90 ± 1.9 mm (range, 73–96 mm) and 63.9 ± 1.1 mm (range, 57–73), respectively, with the snout-vent length of 16 juveniles being 33.8 ± 1.0 (range, 28–44 mm). These lizards tend not to climb, and live in a two-dimensional spatial niche, with all age and sex classes sharing the same microhabitat. The species occupies semi-open habitat with scattered, moderately sized rocks which are used for surveillance and basking. A population in Haiti was found to maintain carefully high, constant body temperatures ($\bar{X}=37^{\circ}\text{C}$) throughout the day, while frequently moving to thermoregulate, feed and socially interact (Marcellini & Jenssen, in press). Burrows and rock crevices serve the lizards as nocturnal retreats and diurnal refugia from predators.

Field observations for the present study were conducted in the north-west corner of the Dominican Republic, 2 km east of Montecristi, from 26 May to 16 June 1988. The study site was a 2800-m² portion of a private club which contained a circle of cabanas, a central pavilion, large (2.5 m in diameter) circular planters, and interconnecting stone walkways bordered by low walls and shrubs. Between these structures were occasional small trees and grass ground cover. This site was chosen because of abundant subjects, habituation of subjects to human activity (diminished observer's effect), the homogenous distribution of habitat available to all subjects, ease of observing the population from the central pavilion, precision of mapping subject position against reference landmarks, and the relative stability of the study site for long-term tracking of resident subjects.

We captured almost all of the lizards on the study site: 13 adult males, 14 adult females and 16 of 24 juveniles. Data recorded for each subject were date and time of capture, site of capture, sex, snout-vent length and body weight. An individual identification number was assigned and recorded for each lizard on a data sheet, as a painted code on the subject's back (sensu Jenssen 1970), and as a permanent toe-clip code. The lizards were then released at their point of capture.

Four kinds of data were gathered. First, periodic censuses were conducted daily for 3 weeks between

0800 and 1700 hours. Each lizard seen during a census was identified and its locality entered on a survey map of the study area by date and time of day. The map localities and focal observations on individual subjects (see below) accumulated 27–108 sightings/resident. These numbers far exceed the 27 sightings recommended by Rose (1982) to depict accurately the home range of *Sceloporus virgatus*, a species with twice the home range area of *L. schreibersi*. Using the locality data, polygons were drawn on a map measuring 55–75 cm which reflected the actual area used by each lizard. The perimeter distance and area of each lizard's polygon (home range) was determined from the map with a Numonics digitizer (model 274–167).

Second, individual adults were continuously observed (focal animal observations; Altmann 1974) for durations of 2–7 h. Data recorded were the time at which a subject moved, the length of the move, the subsequent distances to the nearest conspecific juvenile and adult, and the occurrence of any additional behaviour (e.g. headbob displays, feeding, courtship, copulation, territorial defence). Observations were made on seven male and seven female adults ($\bar{X} \pm \text{SE} = 226 \pm 32$ min/subject).

Third, selected male subjects were tested for the tendency to defend their home range. This was done by placing a conspecific male in a transparent cubicle measuring $3 \times 1.5 \times 1.5$ cm, and then setting the cubicle near a subject in the core of its home range. The response was then videotaped using a Canon camera (model VC 30A) and tape deck (model VR 30A). The subject was considered territorial if it showed aggressive behaviour (erect crest, laterally compressed sides, high amplitude headbobs, approach toward the cubicle), and non-territorial if it did not respond aggressively.

Fourth, experimental observations were made to test the cannibalistic propensity of adult subjects. It is known that other species of *Leiocephalus* will occasionally eat lizards (sauropagous; Schoener et al. 1982). To identify actual cannibalistic subjects from those who will not eat conspecifics, even though there may be a tendency toward saurophagy, the following protocol was used. A stimulus lizard was tethered to a 1-m-long nylon thread affixed to a 2-m pole. The stimulus animals were adult *Anolis distichus* (31–45 mm SVL) and juvenile *L. schreibersi* (31–38 mm SVL) from off the study area. Each subject was presented three stimuli, one per day, in the following order: (1) a conspecific juvenile, (2) an anole and (3) another conspecific

juvenile. The stimulus was set 0.5–2 m from the subject, with the observer backing away to more than 5 m from the subject to watch the response through binoculars. Some portion of the observer (e.g. at least the head) was always in view of the subject. The latency period was recorded between the stimulus presentation and when the subject attempted to grab the stimulus. If an attack did not take place, the trial was terminated after 15 min. A predatory quotient, rating the cannibalistic tendency of the subjects, was established, whereby: 0, no attack on any of the three stimuli; 1, attacked only the anole; 2, attacked the anole and one conspecific juvenile; and 3, attacked all three stimuli. A rank of 0–1 was considered non-predatory on conspecifics and 2–3 indicated a conspecific predator.

Data were entered into an IBM 3081 computer, and statistical descriptions and tests performed with the Statistical Analysis System software program (SAS Institute 1985). All measurements of variance about mean values are \pm SE.

RESULTS

Home Range and Movements

Over the 3-week observation period, all subjects maintained very predictable home ranges, and most adults defended their ranges against conspecifics as indicated by naturally occurring aggression observed during focal observations. Adult male home ranges averaged 46% larger than those of adult females and 92% greater than juvenile home ranges. The respective mean home range areas and perimeters were: for adult males, 78.5 ± 6.0 m² and 51.3 ± 4.9 m; for adult females, 42.5 ± 5.0 m² and 32.5 ± 3.2 m; and for juveniles, 6.3 ± 0.7 m² and 9.6 ± 0.6 m.

Few home ranges were without overlap with other conspecifics (Table I). Only two of 13 adult males had non-overlapping home ranges. Of the adults, females were the most extreme; their home ranges overlapped an average of 88% with male home ranges (no female was without an associated male) and only average a 22% overlap with other females (Table I). Juvenile home ranges were entirely within adult home ranges (96% by females and 100% by males, Table I). The total area occupied by the 24 juveniles on the study site was only 81 m² (about the area of one male home range).

Table I. The mean per cent overlap in home range areas and the mean number of individuals overlapping (in parentheses) among sex and age classes of *L. schreibersi*

Subjects	Adult males	Adult females	Juveniles
13 Adult males	35 (1.5)	35 (1.5)	8 (2.0)
14 Adult females	88 (1.6)	22 (0.9)	11 (1.7)
24 Juveniles	100 (1.1)	96 (1.0)	20 (1.2)

Table II. Total number of moves (M), number of moves after which a nearest neighbour could be seen (N), and the resulting mean separation distance after a move by an adult *L. schreibersi* subject and its nearest juvenile and adult neighbours

Observed subjects	Sample size and nearest neighbour distance (m)					
	M	Juveniles			Adults	
		N	$\bar{X} \pm$ SE	N	$\bar{X} \pm$ SE	
Males						
1*	6	0	—	0	—	
2*	41	0	—	0	—	
3*	65	0	—	30	1.5 ± 0.25	
4	61	0	—	40	2.9 ± 0.29	
5	40	25	1.1 ± 0.14	33	2.5 ± 0.28	
6	84	32	1.1 ± 0.14	58	1.4 ± 0.15	
7	97	8	0.7 ± 0.21	25	1.0 ± 0.29	
Females						
2*	56	0	—	31	1.5 ± 0.21	
3	89	19	1.0 ± 0.18	18	2.4 ± 0.34	
4	77	20	2.3 ± 0.12	64	1.2 ± 0.11	
5	117	92	0.7 ± 0.06	54	2.4 ± 0.31	
6	14	14	0.3 ± 0.05	0	—	
7	62	25	1.0 ± 0.16	18	1.9 ± 0.36	
All subjects	809	235	1.0 ± 0.21	389	2.0 ± 0.24	

Observation durations ranged from 110 to 476 min/subject.

* Denotes conspecific predators.

From examining focal animal observations on movement behaviour, we found no significant differences among the sexes in moves/min (males, $\bar{X} = 0.3 \pm 0.06$; females $\bar{X} = 0.3 \pm 0.09$) or distance travelled/move (males, $\bar{X} = 0.7 \pm 0.10$ m; females, $\bar{X} = 0.6 \pm 0.05$ m). Females were just as active as males, but simply restricted their movements within smaller areas (i.e. home ranges).

Juveniles and adults occupied the same microha-

Table III. Predatory response of adult *L. schreibersi* to tethered stimuli, *A. distichus* and juvenile *L. schreibersi*, giving mean (\pm SE) latency periods (from stimulus presentation to attack) and prey sizes

Stimulus	Predatory quotient*	Sample size	Latency period (min)	Prey size (mm SVL)
<i>A. distichus</i>	2-3	9	1.4 \pm 0.35	39.7 \pm 0.95
	1	7	4.2 \pm 2.40	40.1 \pm 0.74
	0	9	—	38.3 \pm 1.77
<i>L. schreibersi</i>	2-3	16	1.3 \pm 0.54	34.8 \pm 0.62
	0-1	32	—	34.0 \pm 0.42

* Predatory quotient ranks subjects' predatory responses as: 0 = none toward any stimulus; 1: only toward *Anolis*; 2: toward *Anolis* and one *Leiocephalus* trial; and 3: toward *Anolis* and both *Leiocephalus* trials.

bitat and were closely associated. Frequently juveniles and adults were within 1–3 cm of each other, and on several occasions juveniles were seen perched on top of adult females. During focal observations, 47% of moves by nine non-predatory adults stopped within sight of a juvenile, with separation distance averaging 1.0 m regardless of the subject's sex (Table II). No juveniles occurred near the five predatory adults of the sample. In contrast, 54% of adult moves (14 subjects) stopped within sight of another adult, with a mean separation distance of 2.0 m (Table II).

The entire area of juvenile home ranges was completely encompassed by non-predatory adults. Only three juveniles appeared in jeopardy of being eaten due to the potential presence of a predatory adult. Of the total area of juvenile home ranges, 13% was potentially threatened by the occasional presence of a non-territorial adult male and a territorial female (see below).

Predatory Behaviour

Eleven of the 13 adult males were tested for their tendency to attack tethered *A. distichus* adults and *L. schreibersi* juveniles; eight subjects had predatory quotients of 0–1 (non-predators), and three had scores of 2–3 (predators). The home ranges of the untested males did not overlap those of any juveniles; thus, their predatory dispositions were of no consequence to existing juveniles. The 14 adult females were tested; eight had scores of 0–1 and six scored 2–3. Together, nine (36%) of the 25 tested

adults attempted to feed on tethered *L. schreibersi* young.

The responses to the stimulus by predatory adults were unequivocal from those of non-predatory adults. Predatory adults averaged less than 1.5 min to attack either the *L. schreibersi* or *A. distichus* stimulus (Table III). In almost every case the subject charged and grabbed the stimulus without preliminaries. In contrast, non-predatory adults (predatory quotient of 0–1) made no attacks on the *L. schreibersi* stimulus during the 15-min presentation, despite the occasionally vigorous and ungainly struggling by the tethered juvenile. Some of the non-predatory subjects would approach the tethered *L. schreibersi* juvenile, with a few even tongue touching the juvenile, before moving off.

Subjects did not appear to avoid attacking the stimuli because some stimuli were too large to be eaten. As Table III shows, attacked *A. distichus* averaged 40 mm SVL and those not attacked were even smaller, averaging 38 mm SVL. The same was true of the *L. schreibersi* stimuli, where both attacked and ignored juveniles averaged 34 mm SVL.

We examined several natural history variables to see if there were associated differences between predatory and non-predatory adults. Using *t*-tests for significance ($P < 0.05$), we compared snout–vent lengths, home range perimeters and home range areas. No differences were found among females. For males, the three predators were significantly smaller ($\bar{X} = 86 \pm 2.3$ mm SVL) than the non-predators ($\bar{X} = 94 \pm 0.8$ mm SVL); however, due to the small sample, the possible relationship remains tentative. The home range perimeters of predatory males was also significantly larger than non-predatory male-perimeters, and two of these predators were found to be non-territorial (see below); but again, the sample size is too small to make conclusive relationships.

In addition to our staged instances of infanticide, we also saw four cases off the study area where adults had captured and were swallowing conspecific juveniles.

Territorial Behaviour

We observed consensual agonistic behaviour between all adult males on the study area, as well as tested for aggressive responses by placing a transparent cubicle containing a male into a resident's home range. Natural encounters mainly occurred

at the edge of a male's home range where it overlapped with a neighbour's. These encounters were limited to ritualized aggressive signals and only once lead to biting. Before physical contact occurred, one of the antagonists would retreat. With the cubicle tests, aggressive signals were observed, accompanied by an approach to the cubicle. In one instance, the subject collided with the cubicle after a 2-m sprint.

However, there were two adult males, both predators, that differed from the rest in their aggressive behaviour. They were not large adults (86 and 90 mm SVL), yet they had the largest home range perimeters (87 and 78 m) on the study area. Each of their home ranges overlapped (46 and 67%) with three other males, and, when challenged, these two males would retreat. To verify further that the two males were non-territorial, we used the cubicle with an average-sized male. The cubicle was positioned within 3 m of the subjects, but neither subject performed aggressive signals or approached the cubicle in trials lasting 15 min. Thus two of the three predatory males were found to be non-territorial, having broadly overlapping home ranges with other males.

Adult females were also territorial. In contrast to males, their home ranges were smaller and frequently had little or no overlap with those of other females (Table I). We observed the majority of the females on the study area to engage in consensual aggressive encounters; three of these involved biting attacks. Thus females readily defended their home ranges from intrusion by other females.

Risk of Predation

Juveniles were found in the home ranges of non-predatory adults. However, because of overlap in adult home ranges, the most secure juveniles were in home ranges mutually overlapped by on a non-predatory adult male and a non-predatory adult female. The adult of each sex defended its territory against consensual interlopers, and together provided juveniles with protection from both predatory males and females. To quantify the relationship between the presence or absence of juveniles and the predatory disposition of resident adults, we performed the following analysis. The total study site area occupied by adults was divided into four categories: (1) patches mutually occupied by only a non-predatory male and a non-predatory female (safe area); (2) patches occupied by only a single

Table IV. Total study site area used by adult *L. schreibersi* divided into four risk categories for resident juveniles; refer to 'risk of predation' in the Results for definitions

Risk categories	Percentage of category area to total study site area (%)	Juvenile residents within a category (<i>N</i>)	Percentage of category area containing juveniles (%)
Safe patches	28	21	78
Low-risk patches	23	1	4
High-risk patches	25	2	4
Extreme-risk patches	24	0	0

non-predatory adult, or a non-predatory male and non-predatory female with occasional presence of a non-territorial predatory adult (low-risk area); (3) patches mutually occupied by a non-predatory adult and a predatory adult (high-risk area); and (4) patches occupied only by predatory adults (extreme-risk area). Of the resulting mosaic, the proportions of the four kinds of adult areas were approximately equal (Table IV). If juvenile distribution were random, one would expect approximately six juveniles in each of the four areas; however, the distribution was significantly non-random (4×2 contingency table, $P < 0.001$). Safe areas comprised 28% of adult-occupied area on the study site, yet contained 88% of the juveniles (Table IV). Areas of extreme risk (24% of adult-occupied area) contained no juveniles. Furthermore, patches of habitat at low to high risk were almost devoid of juveniles (only 4% of patch areas held juveniles), while safe patches were near saturation (78% of patch areas contained one or more juveniles). The safe areas on the study site were controlled by five pairs of non-predatory adult males and females, and only one of these pairs was without juveniles.

The inference from the above analysis is that a non-predatory male and non-predatory female are a necessary buffer against adult cannibals. The manifestation of this protection is exemplified in the following anecdote. While we were testing a non-predatory female with a juvenile *L. schreibersi* stimulus, a neighbouring predatory female ran out of her home range toward the juvenile. At that moment, our subject moved past the juvenile and aggressively challenged the female intruder. The

non-predatory female chased the predatory female back into the latter's home range and away from the juvenile.

DISCUSSION

Very little is known about *L. schreibersi* beyond its taxonomic and distributional status (Schwartz 1967; Schwartz & Thomas 1975; Etheridge & Queiroz 1988). From our present observations and those of Marcellini & Jenssen (in press), we can profile *L. schreibersi* as being stenothermic, moderate-sized lizards who defend two-dimensional, ground-level territories against conspecifics of their species. Within their hot, semi-open habitat, they are very active, frequently moving and feeding throughout the day within large, stable home ranges. Males are, on average, 30% longer than females, with 45% larger mean home range areas. On average, adult home ranges broadly overlap ($\bar{X}=22-88\%$) with each female residing within a male's home range. Male home ranges partially or completely encompass one to several females. Juvenile home ranges are very small ($\bar{X}=6\text{ m}^2$), and are completely overlapped by adult home ranges. All age and sex classes occupy the same physical niche.

The diet of *L. schreibersi*, as gleaned from focal observations, is similar to that reported for other *Leiocephalus* species (Schoener et al. 1982). Primarily insects were eaten, but we saw lizards feeding on berries and flower parts as well as several individuals who scavenged fallen food scraps at a nearby dining area. Like us, Schoener et al. (1982) observed *Leiocephalus* spp. eating lizards (specifically *Anolis*), but found only two in 216 examined stomachs. The propensity to be a lizard-eater (saurophagous) seems well founded in the genus; however, a wide variety of food types indicates an opportunistic feeding behaviour without any specialization toward saurophagy.

Saurophagous lizard species, such as *Gambelia wislizenii* (e.g. Montanucci 1965, 1967) and various varanids (e.g. Auffenburg 1981; Mitchell 1986), tend to be cannibalistic as well, though some species seem to have adaptations to prevent predation on conspecific juveniles (Rand & Andrews 1975). Unlike that seen in *L. schreibersi*, saurophagy is characterized by low population densities, very large home ranges with little to no territorial defence, and concealed perches from which to carry out predatory ambushes (Stamps 1977).

Our observations and experiments unequivocally show that *L. schreibersi* is both opportunistically saurophagous and cannibalistic, while exhibiting typical insectivorous iguanid social behaviour and spacing patterns (Stamps 1977). Two-thirds of our tested population readily took *Anolis* prey and half of those subjects just as quickly attacked immature conspecifics. Juvenile survival is even more threatened when it is considered that all juvenile home ranges resided within one or more adult home ranges and adult-juvenile separation distances averaged only 1.0 m. This threat posed by spatial intimacy is somewhat unusual as the young of many iguanid species occupy separate microhabitats from those of adults (Heatwole 1977), and thus the potential for cannibalism rarely occurs.

As Glass et al. (1985) pointed out, if some proportion of a population is infanticidal (e.g. cannibalistic), there should be selection for non-infanticidal adults to protect their own fitness; this is usually manifest as some kind of parental care. However, with the exception of crocodylians, no reptiles have been reported to give parental care once progeny have hatched (Shine 1988). Furthermore, there is no evidence that lizards can recognize their offspring (Blaustein et al. 1987). Yet non-predatory *L. schreibersi* may be protecting their genetic fitness by providing their progeny with indirect parental care. The mechanism for this counter-strategy to cannibalism will require more field data to substantiate it, but should be operative if the following conditions exist.

First, a non-predatory, reproductive male and female, sharing territorial defence against conspecifics, would repel potential predatory interlopers. Second, the reproductive male-female pair would have to maintain stable territories for approximately 5 months. This would give the progeny the time for embryonic development and post-hatching growth to a non-vulnerable size for predation (estimated from data on similar species in Andrews 1982). Third, the female of the territorial pair would have to lay her eggs within her territory. Fourth, the hatchlings must have small, stable home ranges established close to their hatching sites. Fifth, for the male's fitness, he would need to be successful in isolating his associated female from insemination by other males.

Some of the life history requirements to provide indirect parental care are already documented, but others remain to be verified. Our evidence demon-

strates a definite predatory and non-predatory disposition among the adult population toward conspecific juveniles. The clumped distribution of juveniles suggests clutchmate associations. Furthermore, each of these areas of juvenile occurrences was associated with non-predatory adults, while no juveniles were found exclusively within predator home ranges. Juvenile home ranges were very small and stable over the 3-week study, suggesting the possibility for long-term site fidelity. Likewise, adult home ranges showed the same stability and were strongly defended by residents. Gathering data on parental relationships between adults and associated juveniles are now of immediate concern.

In summary, we believe that infanticide is institutionalized in *L. schreibersi*, possibly being a prime cause for juvenile mortality. Conspecific predation appears to serve *L. schreibersi* as: (1) exploitation of juveniles directly as food by the predator; (2) elimination of juveniles as competitors with the predator's future offspring; and (3) a density-dependent mechanism for intrinsic population control.

ACKNOWLEDGMENTS

We wish to thank Jose Ottenwalder of the National Zoological Park in Santo Domingo and Enrico Gentile of Las Carabelas in Montecristi for their assistance. The project was generously funded by a Smithsonian Scholarly Studies grant (1235S704) to D.L.M. and T.A.J.

REFERENCES

- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–267.
- Andrews, R. M. 1982. Patterns of growth in reptiles. In: *Biology of the Reptilia. Vol. 13, Ecophysiology* (Ed. by C. Gans & H. F. Pough), pp. 273–320. New York: Academic Press.
- Auffenberg, W. 1981. *The Behavioral Ecology of the Komodo Monitor*. Gainesville, Florida: University of Florida Press.
- Auffenberg, W. & Auffenburg, T. 1988. Resource partitioning in a community of Philippine skinks (Sauria: Scincidae). *Bull. Florida State Mus. Biol. Sci.*, **32**, 151–219.
- Blaustein, A., Bekoff, M. & Daniels, T. 1987. Kin recognition in vertebrates (excluding primates): empirical evidence. In: *Kin Recognition in Animals* (Ed. by D. Fletcher & C. Michener), pp. 333–357. New York: Wiley Interscience.
- Cockburn, A. 1988. *Social Behavior in Fluctuating Populations*. New York: Croon Helm.
- Etheridge, R. & de Queiroz, K. 1988. A phylogeny of Iguanidae. In: *Phylogenetic Relationships of the Lizard Families* (Ed. by R. Estes & G. Pregill), pp. 283–367. Stanford, California: Stanford University Press.
- Fox, L. R. 1975. Cannibalism in natural populations. *A. Rev. Ecol. Syst.*, **6**, 87–106.
- Glass, G. E., Holt, R. D. & Slade, N. A. 1985. Infanticide as an evolutionary stable strategy. *Anim. Behav.*, **33**, 384–391.
- Hausfater, G. & Hrdy, S. B. (Eds) 1984. *Infanticide: Comparative and Evolutionary Perspectives*. New York: Aldine.
- Heatwole, H. 1977. Habitat selection by reptiles. In: *Biology of the Reptilia. Vol. 7, Ecology and Behavior A* (Ed. by C. Gans & D. W. Tinkle), pp. 137–155. New York: Academic Press.
- Hrdy, S. B. & Hausfater, G. 1984. Introduction and overview. In: *Infanticide: Comparative and Evolutionary Perspectives* (Ed. by G. Hausfater & S. Hrdy), pp. XIII–XXXV. New York: Aldine.
- Huntingford, F. A. & Turner, A. K. 1987. *Animal Conflict*. London: Chapman & Hall.
- Jenssen, T. A. 1970. The ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). *J. Herpetol.*, **4**, 1–38.
- Marcellini, D. L. & Jenssen, T. A. In press. Thermal ecology of the tropical iguanid lizard, *Leiocephalus schreibersi*. *Am. Midl. Nat.*
- Mitchell, J. C. 1986. Cannibalism in reptiles: a worldwide review. *Soc. Study Amphib. Rept. Herpetol. Circ.*, **15**, 1–37.
- Montanucci, R. R. 1965. Observations on the San Joaquin leopard lizard, *Crotophytus wislizenii silius* Stejneger. *Herpetologica*, **21**, 270–283.
- Montanucci, R. R. 1967. Further studies on leopard lizards, *Crotophytus wislizenii*. *Herpetologica*, **23**, 119–126.
- Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *A. Rev. Ecol. Syst.*, **12**, 225–251.
- Polis, G. A. & Myers, C. A. 1985. A survey of intraspecific predation among reptiles and amphibians. *J. Herpetol.*, **19**, 99–107.
- Polis, G. A., Myers, C. A. & Hess, W. 1984. A survey of intraspecific predation within the class Mammali. *Mammal. Rev.*, **14**, 187–198.
- Rand, A. S. & Andrews, R. M. 1975. Adult color dimorphism and juvenile pattern in *Anolis cuvieri*. *J. Herpetol.*, **9**, 257–260.
- Rose, B. 1982. Lizard home ranges: methodology and functions. *J. Herpetol.*, **16**, 253–269.
- SAS Institute. 1985. *SAS User's Guide: Statistics, Version 5*. Cary, North Carolina: SAS Institute.
- Schwartz, A. 1967. The *Leiocephalus* (Lacertilia, Iguanidae) of the southern Bahama Islands. *Ann. Carnegie Mus.*, **39**, 153–185.
- Schwartz, A. & Thomas, R. 1975. A checklist of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist. Spec. Publ.*, **1**, 1–216.
- Schoener, T. W., Slade, J. B. & Stinson, C. H. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus*, of the Bahamas. *Oecologia (Berl.)*, **53**, 160–169.

Shine, R. 1988. Parental care in reptiles. In: *Biology of the Reptilia. Vol. 16, Ecology B* (Ed. by C. Gans & R. B. Huey), pp. 275–330. New York: Academic Press.

Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. In: *Biology of the Reptilia. Vol. 7, Ecology*

and Behavior A (Ed. by C. Gans & D. W. Tinkle), pp. 265–334. New York: Academic Press.

(Received 9 December 1988; revised 16 February 1989;
MS. number: A5447)